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Sweetening responses of potato tubers of different maturity to conventional and non-conventional storage temperature regimes

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ABSTRACT

Low storage temperatures stimulate the accumulation of glucose and fructose (sweetening) in potato (*Solanum tuberosum* L.) tubers, resulting in unacceptably dark processed products during frying. Information on how tubers respond to unorthodox storage temperature regimes is lacking, especially for the relatively new frozen-processing cultivars, 'Umatilla Russet' and 'Ranger Russet'. Such knowledge could greatly facilitate the ability to manage immature, over-mature, or otherwise stressed potatoes. This study characterizes the sweetening responses of 'Russet Burbank', 'Ranger Russet' and 'Umatilla Russet' tubers of different maturity, over a range of conditioning and holding storage temperatures. Tubers from early- and late-planted crops were wound-healed (12 °C) for 17 d after harvest (DAH), conditioned for a month (17–48 DAH) at 4.5, 6.7, or 9 °C, and subsequently stored (48–230 DAH) at 4.5, 6.7 or 9 °C (nine temperature regimes) for an additional 182 d before reconditioning at 16 °C for 21 d. Reconditioning hastens catabolism of reducing sugars and restoration of processing quality. On average, tubers from the early planting had lower rates of respiration during wound-healing and emerged from dormancy sooner than those planted later, indicating relative immaturity of the latter. The early-planted crop of 'Ranger Russet' was more sensitive to low temperature sweetening than the late-planted crop, reflecting a tendency of tubers to become over-mature and reinforcing the benefit of a 'green' harvest for this cultivar. All cultivars sweetened rapidly when conditioned at 4.5 °C. Conditioning at 6.7 and 9 °C, however, decreased the extent of low temperature sweetening during subsequent storage at 4.5 °C through most of the storage season, expanding the options for managing potatoes with lower than normal temperature later in storage. The processing quality of 'Ranger Russet' was maintained for 230 d with higher conditioning/holding temperature regimes. Reducing sugar concentrations in cold-sweetened 'Ranger Russet' and 'Russet Burbank' tubers decreased more than in 'Umatilla Russet' tubers in response to reconditioning at 16 °C. Following an interval of wound-healing, the use of combinations of non-conventional conditioning and holding temperatures that do not stimulate excessive sweetening broadens the management options for storing potatoes for the frozen-processing industry.

1. Introduction

Long-term storage of potato tubers presents several challenges, including disease and sprout control, minimizing shrinkage, and maintenance of processing quality. One of the most important factors affecting all of these processes is temperature. A typical storage temperature for potatoes for the frozen-processing industry is 8–9 °C, representing a compromise between lower temperatures which minimize pathogen development and prolong dormancy, and higher temperatures which ensure desirable carbohydrate levels for processing. Glucose and fructose (reducing sugars) accumulate in tuber tissue below about 7 °C, rendering tubers unacceptable for processing into French fries when they collectively reach or exceed about 2.6% of tuber dry weight (Driskill et al., 2007). Reducing sugars react with free amino acids during processing, resulting in dark colored fries and chips (Scallenberger et al., 1959) that are relatively high in acrylamide (Amrein et al., 2003). To some extent, these accumulated sugars can be reduced by a brief reconditioning period at a higher temperature prior to processing, although the effectiveness of reconditioning depends on cultivar and the duration of storage.

In addition to temperature, the physiological maturity of a crop at harvest has been shown to affect postharvest carbohydrate metabolism (Miller et al., 1975; Pritchard and Adam, 1992). Hertog et al. (1997a) found that for a series of weekly harvests, reducing

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sugar synthesis during 4 °C storage declined progressively with increasing tuber maturity. Moreover, harvesting either earlier or later in the season can have an impact on the ultimate storage life through effects on tuber maturity that are cultivar-specific (Nelson and Sowokinos, 1983).

A single holding temperature, selected in accordance with end-use and which balances the concerns discussed above, is usually recommended for long-term storage of potatoes. The critical temperature at which sweetening and thus loss of processing quality occurs is cultivar-dependent and needs to be determined for newer releases. Information on the reconditioning abilities of specific cultivars is also important, as reducing sugars can increase, even at the most ideal storage temperatures, due to in-season stresses (e.g. water, temperature) that are not readily apparent at harvest (Eldredge et al., 1996). While it is generally accepted that potatoes should be fully "mature" before entering storage, a quantifiable indicator for physiological maturity is lacking and may vary among cultivars.

The potato cultivars 'Ranger Russet', 'Umatilla Russet', 'Russet Burbank', and 'Shepody' dominate the frozen French fry processing industry in the Pacific Northwest. Shepody is normally processed immediately after harvest, whereas 'Russet Burbank' is the choice for long-term storage. 'Ranger Russet' (Pavek et al., 1992) and 'Umatilla Russet' (Mosley et al., 2000) are fairly recent releases that were bred to replace, or improve upon, the existing cultivars. In general, 'Ranger Russet' and 'Umatilla Russet' do not maintain postharvest processing quality as long as 'Russet Burbank' and therefore dominate the raw product supply to processors earlier in the storage season.

Virtually nothing is known about the effects of tuber maturity on the long-term storability of 'Ranger Russet' and 'Umatilla Russet'. A major challenge for storage managers is to accurately estimate the physiological condition of a crop coming into storage so that storage conditions can be modified accordingly, to best preserve processing quality for the desired storage duration. For example, depending on crop condition, "it may be necessary to cool and hold processing potatoes well below the cultivar-specific limits typically recommended for frozen processing" (McMorran et al., 2008). Varying the temperature regimes after wound-healing could be an effective management practice to extend the processing window by controlling respiration, disease development, desiccation, and sprouting. A recent review of techniques for handling and storing problem potatoes is available (Knowles and Plissey, 2008). Information on how newer processing cultivars respond to various storage temperature regimes (sequences of higher and lower than normal temperatures) is lacking. Such information could greatly facilitate the ability to manage problem potatoes (e.g. wet, blighted, frozen, wounded, heat stressed) or potatoes that are less than ideal maturity.

Planting dates were manipulated in the studies reported herein to create two physiological maturities of 'Ranger Russet', 'Umatilla Russet' and 'Russet Burbank' tubers. Various physiological attributes of the tubers were then measured following harvest to identify markers of maturity that might subsequently help to explain differences in storage behavior. Options for short-, medium-, and long-term storage were explored by pairing various preliminary (conditioning) temperatures with different holding temperatures while monitoring changes in reducing sugar levels in all cultivars and maturities throughout a 230-d postharvest period. Specific questions included: To what extent does tuber maturity affect sweetening? Given differences in tuber maturity at harvest, can storage temperature regimes be identified that will limit the sweetening responses of 'Ranger Russet' and 'Umatilla Russet' for prolonged periods? What are the reconditioning potentials of these cultivars following a period of prolonged storage?

2. Materials and methods

2.1. Field plot design and maintenance

Each year of the study, cut seed (50–65-g seedpieces) of 'Ranger Russet', 'Russet Burbank', and 'Umatilla Russet' certified (G-3) seed-tubers (*Solanum tuberosum* L.) were obtained from a local seed potato packing shed in early April. The seed was held at 10 °C (95% RH) until planting. Planting dates were approximately 15 April ("Early") and 15 May ("Late") of each year (2002–2004) at the Washington State University Irrigated Agriculture Research and Extension Center at Othello, WA (46°47.277′N. Lat., 119°2.680′W. Long.). The planting dates were varied to achieve different tuber maturities at harvest, which occurred on 25 September each year. Treatments were arranged in a split plot design, with planting date as mainplot and cultivar as subplots (five replicates).

Seedpieces were planted 20-cm deep in a Shano silt loam soil [classified as Andic Mollic Camborthid (Lenfesty, 1967)] with a custom built two-row assist-feed planter. Treatment plots were 6 m long and consisted of 24 seedpieces planted 25 cm apart within a row, with a 1-m alley at the end of each plot. Rows were 86 cm apart. Guard seedpieces (cvs. Dark Red Norland or Chieftan) were planted at the beginning and end of each plot to minimize the variation in interplant competition for plants at the ends of plots, and to facilitate the separation of individual plots during mechanical harvesting in the fall. Guard rows of 'Russet Burbank' flanked each experimental row to maintain a uniform level of competition for each cultivar. Plots were located under a linear move irrigation system. Soil moisture was maintained at a minimum of 65% of field capacity with the aid of soil moisture probes positioned throughout the field. Pre-plant and in-season fertilizer applications were based on soil tests and petiole analyses, respectively, following standard practices for long-season russet potatoes in the Columbia Basin. Herbicides, insecticides and fungicides were applied as needed. Vines were removed using a flail-type mower in mid September to allow approximately 13 d for tuber maturation before harvest.

Tubers were harvested with a single-row mechanical harvester, approximately 163 and 133 d after planting (DAP) for the early and late plantings, respectively. Tubers were washed, weighed, counted, and sorted into the following categories: under 113 g, 113–170 g, 170–284 g, 284–340 g, 340–397 g, over 397 g, and culls. Total yield included the combined weights of all categories, U.S. number one yield was equal to the sum of all categories except cull and undersize (<113 g) tubers, and marketable yield included U.S. number one plus undersize tubers. The 171–284-g tubers were transported to the Washington State University Postharvest research lab in Pullman, WA for maturity assessments and storage studies. While the experiments were conducted over three growing seasons (2002–2004) to provide tubers for subsequent storage studies (see below), the effects of planting date and cultivar on yield and tuber size distribution were analyzed in 2003 and 2004 only.

2.2. Indices of tuber maturity

2.2.1. Respiration and specific gravity

Basal respiration rates of tubers from the early and late plantings were measured over a 14-d wound-healing period at 12 °C (95% RH) immediately following harvest. Eighteen tubers from each cultivar and planting date (maturity) were blocked for size (230–250 g per tuber) and sealed in 3.8 L glass chambers (six tubers per chamber) equipped with inlet and outlet ports. There were three replicates of each treatment (3 cultivars × 2 planting dates). Humidified (95% RH) airflow to each chamber averaged 120 mL min^{-1} of CO_2-free air. The outflow from each chamber was directed through an LI-6262 infrared gas analyzer (LI-COR, Inc., Lincoln, Nebraska) by a three

way solenoid valve controlled by a computer. Carbon dioxide concentrations were recorded every 6 h for each treatment over the 14-d wound-healing period and respiration rates are reported as mg CO_2 kg^{-1} h^{-1}. Tuber specific gravities were measured at the end of the wound-healing period for the three replicates of each cultivar and planting date by the weight in air/weight in water method (Gould, 1999).

2.2.2. Dormancy

Following completion of the respiration study, tubers were removed from the chambers and placed at 9 °C (95% RH) in darkness to determine length of dormancy. Sprout length measurements were taken every seven days. The length of the longest sprout on each of the six tubers for each treatment (cultivar and planting date) was recorded (three replicates). Readings were terminated when the cumulative length of the longest six sprouts exceeded 20 cm for a particular cultivar and planting date. Sprout length data were plotted versus days after harvest. Tubers were considered to have broken dormancy when average sprout length was ≥1.7 mm.

2.2.3. Carbohydrate analyses

Sucrose, glucose and fructose concentrations were quantified in tubers from the early and late plantings at 17 d after harvest, immediately following wound-healing. Twelve tubers of each cultivar/maturity combination were sampled in four replicates of three tubers each. A central slice (approximately 1.5 mm thick, periderm attached) along the apical to basal axis of each of the three tubers of a given treatment were collectively frozen at −80 °C and lyophilized. The dried tissue was ground with a mortar and pestle and sieved through a 60 mesh (0.246 mm) screen. For carbohydrate analyses, 500 mg of lyophilized tissue were extracted in 6 mL of triethanolamine HCl (TEA) buffer (30 mM, pH 7.0) followed by successive additions of 300 μL of 85 mM $K_4[Fe(CN)_6]\cdot 3H_2O$ (Carrez I), 300 μL of 250 mM $ZnSO_4\cdot 7H_2O$ (Carrez II), and 500 μL of 0.1 mM NaOH with vortexing after each addition. The extract was centrifuged (10,000 × g) for 15 min and the supernatant was stored at −20 °C until required.

Glucose and fructose were estimated according to a microplate modification of Bergmeyer et al. (1974) and Bernt and Bergmeyer (1974). The stoichiometric reduction of NADP as each hexose is converted to 6-phosphogluconate was monitored at A_{340}. Extracts were diluted to a concentration of less than 1.0 mM each glucose, fructose and sucrose. An aliquot of 30 μL was diluted with 160 μL of 0.3 M TEA buffer (pH 7.4) containing 20.6 μM ATP, 1.6 μM NADP and 3 mM $MgSO_4$. For determination of free glucose, 10 nkat each of glucose-6-phosphate dehydrogenase and hexokinase were added simultaneously and the absorbance was measured after 15 min incubation. Phosphoglucose isomerase (17 nkat) was then added and the extracts were incubated for 30 min before measuring absorbance for the quantitation of fructose. A separate sample of the extract was pre-treated for 30 min with 14 nkat invertase in 0.1 M acetate buffer (pH 4.6) for the determination of total glucose (free glucose plus that hydrolyzed from sucrose via invertase). The difference between moles total glucose and moles free glucose was used as a measure of sucrose (Bergmeyer and Bernt, 1974). All steps were carried out at room temperature. Quantitation was based on standard curves of glucose, fructose and sucrose (0.05–2.4 mM).

2.2.4. Processing quality

Tubers stored for 31 d at 6.7 °C following a 17-d wound-healing period at 12 °C were evaluated for fry color. Strips (9.5-mm-thick × 2.9-cm-wide × length of tuber) were cut along the apical to basal axis from each of 12 tubers. The strips (one from each tuber) were collectively fried in 191 °C vegetable oil for 3.5 min. The color (lightness) of the basal and apical ends of each strip was then measured with a Photovolt (Model 577, Photovolt Instruments Inc., Indianapolis, IN) reflectance meter within 3 min of frying (Knowles and Pavek, 2004).

2.3. Temperature grid study

A temperature grid protocol (Driskill et al., 2007) was used to assess the effects of a broad range of storage temperatures on the reducing sugar accumulation responses of tubers from the early and late plantings. This approach assesses how various combinations of initial conditioning and subsequent holding temperatures interact to affect the longevity and processing qualities of tubers of different maturities. Following a 17-d healing period at 12 °C (95% RH), tuber reducing sugar concentrations were measured and the remaining tubers were distributed among 4.5, 6.7 and 9 °C storage conditions to condition for 31 d (12 October–12 November). Tubers were again sampled for reducing sugar analysis on 12 November (48 DAH) and tuber samples from each conditioning temperature were transferred to 4.5, 6.7 and 9 °C holding temperatures. Tuber reducing sugar concentrations were measured on 14 January, 13 March, and 13 May (111-, 169-, and 230-DAH) during the 182-d holding period in each year of the three-year study. The study thus consisted of three conditioning temperatures factorially arranged with three holding temperatures for a total of nine storage temperature regimes (conditioning temperature × holding temperature combinations) for tubers from the early and late plantings of each cultivar (18 treatments for each cultivar).

To assess reconditioning potential, all tubers were placed at 16 °C (95% RH) on 13 May where they remained until 3 June (21 d). Reducing sugar concentrations were assessed at the end of the reconditioning period. Hence, the entire storage period of 251 d included 17 d of curing, plus 31 d of conditioning, followed by storage at holding temperatures for 182 d, and subsequent reconditioning for 21 d. Tubers were treated with 3-nonen-2-one (Bedoukian Research Inc., Danbury, CT) at a rate of 0.75 mmol kg^{-1} tuber to inhibit sprouting as needed (≤2 applications) over the 251-d storage interval (Knowles and Knowles, 2007). The compound was applied to filter paper placed on top of tubers in a 190 L plastic chamber. A fan below the pile circulated vapors in the sealed chamber for 24 h. Three such grid studies were completed annually, one each for 'Russet Burbank', 'Ranger Russet' and 'Umatilla Russet' tubers during the 2002, 2003 and 2004 storage seasons.

2.4. Data analysis and presentation

The effects of cultivar and planting date on tuber yields and grades (tuber size distributions) were evaluated. Data were subjected to analysis of variance (ANOVA) and sums of squares were partitioned into single degree-of-freedom contrasts for main effects (cultivar and planting date) and interactions, as appropriate. Tuber size distribution differences for the early and late plantings of each cultivar are summarized in polygonal plots. The effects of planting date on the initial indices of tuber maturity following harvest (sucrose, reducing sugars, specific gravity, 48 d basal end fry color, respiration rates, and dormancy length) were analyzed separately for each cultivar and, where significant, data are reported with associated *P*-values. Except for 2002, where changes in respiration rates of tubers from the early and late plantings were plotted versus time to provide an example of the trends during wound-healing, respiration rates were averaged over the 2-week wound-healing periods and over years to define the main effect of planting date for each cultivar. The effects of planting date, storage time, conditioning temperature (CT), holding temperature (HT), and their interactions on reducing sugar content of tubers were partitioned in ANOVA separately for each cultivar. Changes in reducing

Table 1
Tuber yields from cvs. Russet Burbank, Ranger Russet and Umatilla Russet as affected by planting date. Tubers were harvested on 25 September (163 and 133 d after planting) from early (15 April) and late (15 May) plantings at Othello, WA. Data are averaged over the 2003 and 2004 growing seasons.

Cultivar	Planting date	Tuber Yield ($t\,ha^{-1}$)			Tubers/ha (1000s)	Tuber F. wt. (g/tuber)[a]
		Total	U.S. #1	Marketable[a]		
Russet Burbank	4/15	67.5	51.2	60.2	320	199
	5/15	65.1	51.6	58.2	323	182
Ranger Russet	4/15	86.3	74.0	81.6	378	216
	5/15	63.8	52.8	61.2	350	175
Umatilla Russet	4/15	77.8	60.0	73.3	470	155
	5/15	65.5	51.5	60.6	351	173
$LSD_{0.05}$		2.6	2.6	2.6	39	15.4
Cultivar (CV)		***	***	***	***	***
Planting date (PD)		***	***	***	***	**
CV × PD		***	***	***	***	***

[a] U.S. #1 + <113 g.
** $P \leq 0.01$.
*** $P \leq 0.001$.

sugar concentrations in response to CT and HT are plotted ±SE versus storage time. Since trends were similar from year to year, three-year averages are presented.

3. Results

3.1. Yield responses to planting date

Total, U.S. No. 1, and marketable tuber yields from the late planting of 'Ranger Russet' and 'Umatilla Russet' were significantly lower than from the early planting (Table 1). The early planting of 'Ranger Russet' produced 20.4 $t\,ha^{-1}$ more yield of marketable tubers than the late planting and all of this increase was attributable to tubers larger than 284 g (Fig. 1). Similarly, the early planting of 'Umatilla Russet' produced 12.7 $t\,ha^{-1}$ more marketable yield than the late planting; however, unlike 'Ranger Russet', this difference was due to an increase in yield of tubers less than 284 g. The planting date-induced shift in tuber size distribution of 'Umatilla Russet' toward smaller size tubers (Fig. 1) was at least partly due to an effect on tuber set, as evidenced by 119,000 more tubers per hectare produced by the early planting (Table 1). Furthermore, this effect of planting date on tuber set was unique to 'Umatilla Russet' and was not due to differences in plant stand (data not shown). Total, U.S. No. 1, and marketable yields of 'Russet Burbank' were not affected by planting date, but average tuber size was 9.3% higher for the early planting, reflecting a significant shift in tuber size distribution in favor of larger (>397 g) tubers at the expense of smaller grades over the longer growing period (Fig. 1).

3.2. Physiological and chemical indices of maturity

Physiological and chemical indicators of maturity were assessed soon after harvest for tubers from the planting date studies (Table 2). Across cultivars, sucrose concentrations were highest in tubers from the late plantings. This effect was greatest for 'Ranger Russet' tubers, where tubers from the late planting had a 38% higher concentration of sucrose than those from the early planting. 'Ranger Russet' tubers from the late planting also had higher specific gravity than those from the early planting. Planting date had no effect on the color of French fries (stem end Photovolt reflectance) from 'Russet Burbank' and 'Umatilla Russet' tubers conditioned at 6.7 °C for 31 d. In contrast, French fries from the late planting of 'Ranger Russet' were significantly lighter (USDA 1) than from the early planting (USDA 2). The concentration of reducing sugars in 'Umatilla Russet' tubers from the late planting was 115% higher than in tubers from the early planting at 17 DAH.

As illustrated by the 2002 crop, respiration rates of 'Ranger Russet', 'Russet Burbank', and 'Umatilla Russet' tubers were relatively high following harvest but declined rapidly over the 14-d wound-healing interval at 12 °C (Fig. 2). This basic trend was con-

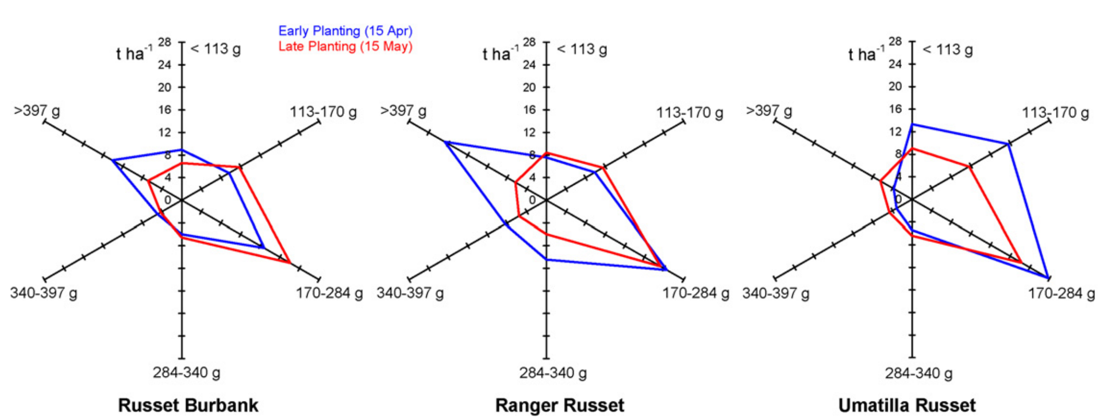

Fig. 1. Polygonal plots showing the effects of planting date on the tuber size distributions produced by 'Russet Burbank', 'Ranger Russet', and 'Umatilla Russet' potatoes in the Columbia Basin of WA. Yield axes range from 0 to 28 $t\,ha^{-1}$. The area encompassed by each polygon is indicative of total marketable yield (U.S. No. 1 + <113 g tubers). Changes in shape or shifts in position of the polygons characterize an effect of planting date on tuber size distribution. Total, U.S. No. 1, and marketable yields, along with tuber number and average tuber weights are given in Table 1 with a statistical summary. Data are averaged over the 2003 and 2004 growing seasons. Plots were harvested on 25 September, 163 and 133 d after planting for the 15 April and 15 May planting dates, respectively.

Table 2
Effects of planting date on chemical and physiological indices of tuber maturity. Tubers (227–284 g) were harvested 25 September from early (15 April) and late plantings (15 May) of cvs. Russet Burbank, Umatilla Russet and Ranger Russet potatoes at Othello, WA. Data are averaged over three growing seasons (2002–2004) unless otherwise noted.

Maturity indicators	Russet Burbank		Umatilla Russet		Ranger Russet	
	Early	Late	Early	Late	Early	Late
Sucrose (mg g^{-1} dry wt)	5.48	7.02*	7.33	9.10*	6.96	9.61**
Glu + Fru (mg g^{-1} dry wt)	3.98	5.02	2.49	5.35***	4.81	4.35
Specific gravity[a]	1.077	1.076	1.088	1.089	1.079	1.086***
Stem end reflectance[b] (31 d at 6.7 °C)	18.9	19.6	29.6	30.5	24.0	28.1**
Tuber respiration[c] (mg CO_2 kg^{-1} h^{-1})	4.06	5.09**	4.66	5.67**	4.64	4.90
Dormancy (days to 1.7-mm sprouts)	138	146	104	119*	79	92*

Suc, Glu, Fru were analyzed 17 d after harvest. Respiration rates are averaged over 14 d of healing at 12 °C immediately following harvest. The duration of dormancy was assessed in tubers stored at 9 °C following wound-healing.

[a] 2002 season only.

[b] Photovolt readings ≥31 = USDA 0, 25–30 = USDA 1, 20–24 = USDA 2, 15–19 = USDA 3, ≤14 = USDA 4.

[c] RR and RB 2002 and 2004 only.

* $P \le 0.05$ level.

** $P \le 0.01$ level.

*** $P \le 0.001$ level.

sistent from year to year. Averaged over years, planting date had no effect on the respiration rate of 'Ranger Russet' tubers during wound-healing (Table 2). However, respiration rates of 'Russet Burbank' and 'Umatilla Russet' tubers from the late planting were consistently 25% and 22% higher, respectively, than those from the early planting, characterizing a difference in physiological status of the tubers (see also Fig. 2). In 2002 and 2004, tubers from the early planting of all cultivars broke dormancy sooner than tubers planted later (Fig. 3). This effect of planting date on dormancy break of 'Ranger Russet' and 'Umatilla Russet' was also evident in 2003; however, tubers from the late planting of 'Russet Burbank' emerged from dormancy earlier in 2003 than those from the early planting. Hence, when averaged over three years, the length of dormancy of 'Russet Burbank' tubers was not affected by planting date (Table 2).

Table 3
Levels of significance (*P* values) for treatments affecting reducing sugar (Glu + Fru) concentrations in tubers stored under nine combinations of conditioning and holding temperatures in the temperature grid study (three-year average, 2002–2004 storage seasons). Changes in reducing sugar concentrations are shown in Figs. 4–7.

Sources of variation for reducing sugars	Ranger Russet	Umatilla Russet	Russet Burbank
Planting date (PD)	0.001*	ns	0.001
Storage time (DAH)	0.001	0.001	0.001
Conditioning temperature (CT)	0.001	0.001	0.001
Holding temperature (HT)	0.001	0.001	0.001
PD × DAH	0.01	0.001	0.001
PD × CT	ns	ns	ns
PD × HT	ns	ns	0.001
CT × DAH	0.001	0.001	0.001
CT × HT	0.05	0.01	0.001
HT × DAH	0.001	0.001	0.001
PD × CT × DAH	ns	ns	ns
PD × HT × DAH	0.01	0.05	0.01
PD × CT × HT	ns	ns	ns
CT × HT × DAH	ns	ns	0.01
PD × CT × HT × DAH	ns	ns	ns

* Levels of significance ($P \le$) for indicated sources of variation (ns, not significant).

3.3. Storage temperature regime studies

3.3.1. cv. Ranger Russet

Changes in reducing sugar concentrations of 'Ranger Russet' tubers from the early and late plantings in response to storage temperature regimes are shown in Fig. 4 and the statistical summary is given in Table 3. Tuber reducing sugar concentrations were affected by planting date, storage time, conditioning temperature, and holding temperature. When held at a constant storage temperature after wound-healing, sweetening of 'Ranger Russet' tubers increased as storage temperature decreased (Fig. 4A and E). Moreover, regardless of planting date, the sweetening responses of tubers to lower temperatures (4.5 and 6.7 °C) occurred rapidly, with maximum reducing sugar concentrations reached within the first month of storage.

As expected, reducing sugar concentrations increased as the initial conditioning temperature (12 October–12 November) was reduced from 9 to 4.5 °C for tubers from both the early and late

Table 4
Rates of increase in reducing sugars (Glu + Fru) as affected by storage conditioning temperatures (12 October–12 November, see Figs. 4, 6, and 7). Average of three storage seasons (2002–2004).

Conditioning temperature (°C)	Cultivar and planting date					
	Ranger Russet		Umatilla Russet		Russet Burbank	
	Early	Late	Early	Late	Early	Late
	Reducing sugar accumulation rates (μg g^{-1} dry wt d^{-1})					
9	120	37	127	84	102	149
6.7	313	290	296	282	516	585
4.5	874	819	658	835	1068	1223
PD	ns		ns		ns	
Temperature	**		**		**	
PD × Temp	*		*		ns	

PD, planting date. ns, not significant.

* $P \le 0.05$ level.

** $P \le 0.01$ level.

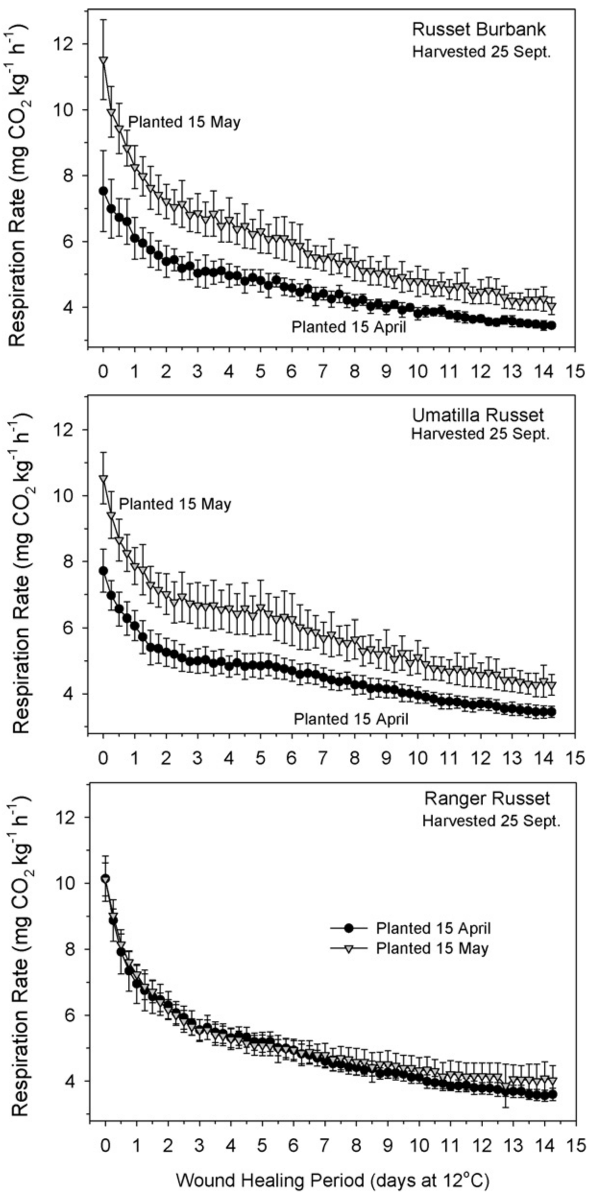

Fig. 2. Effects of planting date on the respiration rates of 'Russet Burbank' (top), 'Umatilla Russet' (middle), and 'Ranger Russet' (bottom) tubers during a 2-week wound-healing period at 12 °C (95% RH) directly following harvest (25 September 2002). Similar size tubers (230–250 g per tuber) were placed in open airflow chambers in the dark and CO_2 concentration was recorded by an infrared gas analyzer at 6-h intervals. Each point is the average ±SE of 18 tubers. Planting date, $P \leq 0.01$.

plantings (Fig. 4B–D and F–H). Across planting dates, average rates of reducing sugar accumulation (dry wt basis) for 'Ranger Russet' tubers conditioned at 4.5, 6.7, and 9 °C were 847, 302, and 79 $\mu g\,g^{-1}\,d^{-1}$, respectively, during the month-long conditioning period (Table 4). Hence, the rate of reducing sugar accumulation decreased by 170 $\mu g\,g^{-1}\,d^{-1}$ ($P \leq 0.05$) for every degree centigrade increase in conditioning temperature. While reducing sugar accumulation rates were not affected by planting date in tubers conditioned at the lower temperatures (4.5 and 6.7 °C), tubers from the early planting sweetened 3.2-fold faster ($P \leq 0.02$) than those from the late planting when conditioned at 9 °C (Table 3, PD × Temp ≤0.05). This difference is clearly evident in Fig. 4D and H.

The levels of reducing sugars during the holding period depended on temperature, with higher relative concentrations at lower temperatures regardless of conditioning temperature and planting date (Fig. 4; Table 3, HT × DAH, $P \leq 0.001$). However, the absolute levels of reducing sugars in tubers held at the lowest holding temperature of 4.5 °C were reduced over the first 120 d of the holding period (from 48 to 169 d) for tubers conditioned at 6.7 or 9 °C during the initial month following wound-healing (CT × HT, $P \leq 0.05$) (Fig. 4C, D, G, and H). Moreover, the high reducing sugar concentrations in tubers conditioned at 4.5 °C were reduced significantly when storage temperatures were subsequently raised to 6.7 and 9 °C for the remainder of the 230-d storage period (Fig. 4B and F).

On average, tubers from the early planting accumulated higher concentrations of reducing sugars than those from the late planting during storage (PD × DAH, $P \leq 0.01$, Table 3). The effects of planting date on sweetening, however, were somewhat dependent on the

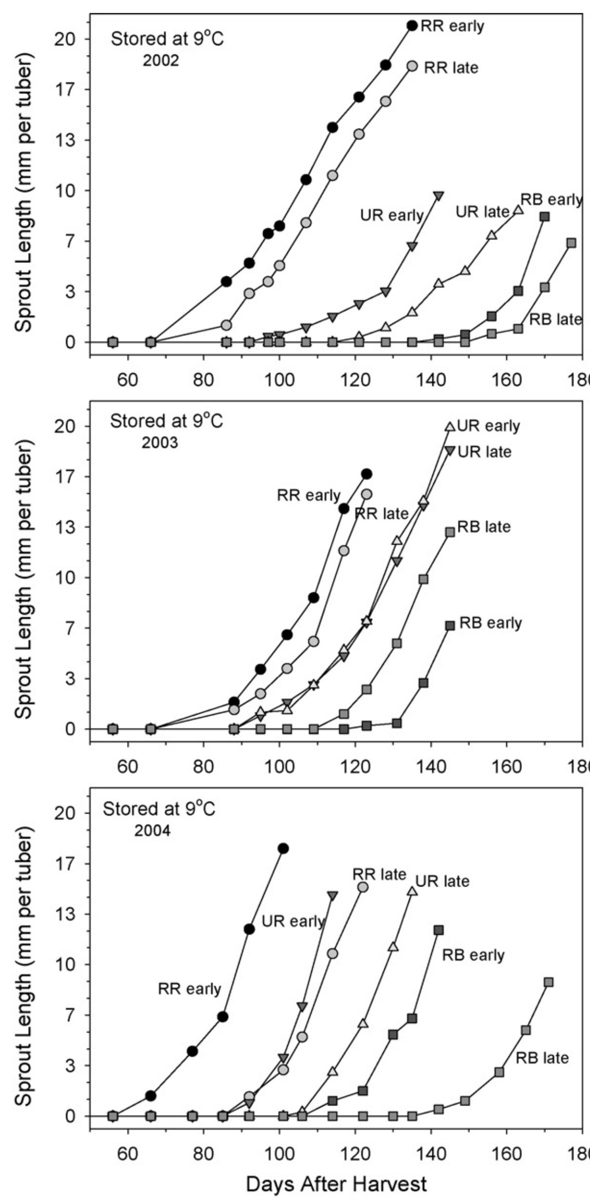

Fig. 3. Effects of planting date (15 April = early; 15 May = late) on emergence from dormancy and sprouting of 'Ranger Russet', 'Umatilla Russet' and 'Russet Burbank' tubers. The tubers were harvested 25 September, 163 and 133 d after planting for the early and late harvests, respectively. Following a 17-d wound-healing period at 12 °C, the tubers were placed at 9 °C (95% RH) in the dark and sprout length was measured (mm) at weekly intervals. Each point is the average of 18 tubers.

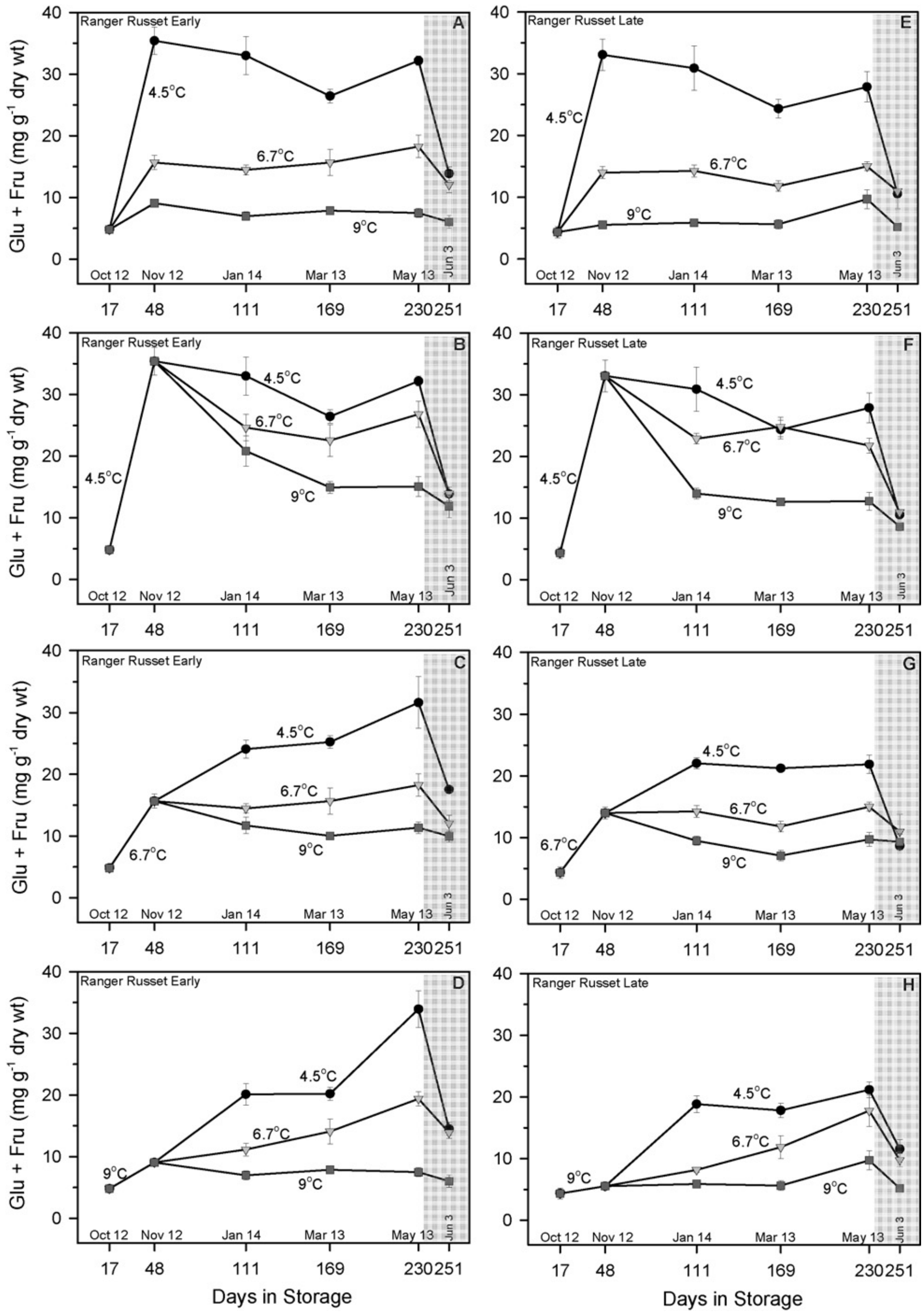

Fig. 4. Changes in reducing sugar (glucose + fructose) concentrations in 'Ranger Russet' tubers of different maturity (planting date) in response to conditioning, holding, and reconditioning temperatures over 251 d of storage. Tubers from early (left column) and late plantings (right column) were harvested 25 September (163 and 133 d after planting), wound-healed at 12 °C (95% RH) for 17 d, and then placed at 4.5, 6.7 and 9 °C to condition for 31 d (12 October–12 November). Tuber samples from each conditioning temperature were subsequently stored at 4.5, 6.7 and 9 °C (holding) for an additional 182 d (until 13 May), resulting in nine conditioning/holding temperature combinations. Tubers were reconditioned (shaded) for 21 d at 16 °C (13 May–3 June) at the end of the study. Data are averaged over three storage seasons (n = 36, ±SE). ANOVA results are presented in Table 3.

holding temperature (PD × HT × DAH, $P \leq 0.01$). From 48 to 230 d after harvest (DAH), tubers from the early planting experienced a sharp rise in reducing sugar concentration at 4.5 °C late in the storage season relative to those from the late planting (Figs. 4 and 5). Cold-sweetened tubers of 'Ranger Russet' reconditioned well when the storage temperature was increased to 16 °C, with reducing sugar concentrations decreasing to 15 mg g^{-1} dry wt (USDA 1) or less for most of the treatments over the 21-d interval (230–251 DAH) (Fig. 4).

3.3.2. cv. Umatilla Russet

Similar to 'Ranger Russet', reducing sugar concentrations of 'Umatilla Russet' tubers were affected by planting date (in various interactions), storage time, conditioning temperature, and holding temperature (Table 3). Sweetening of 'Umatilla Russet' tubers increased as storage temperature decreased, with close to maximum sugar concentrations reached within the first month of storage (Fig. 6A and E). Reducing sugar concentrations increased in tubers as the initial conditioning temperature (12 October–12

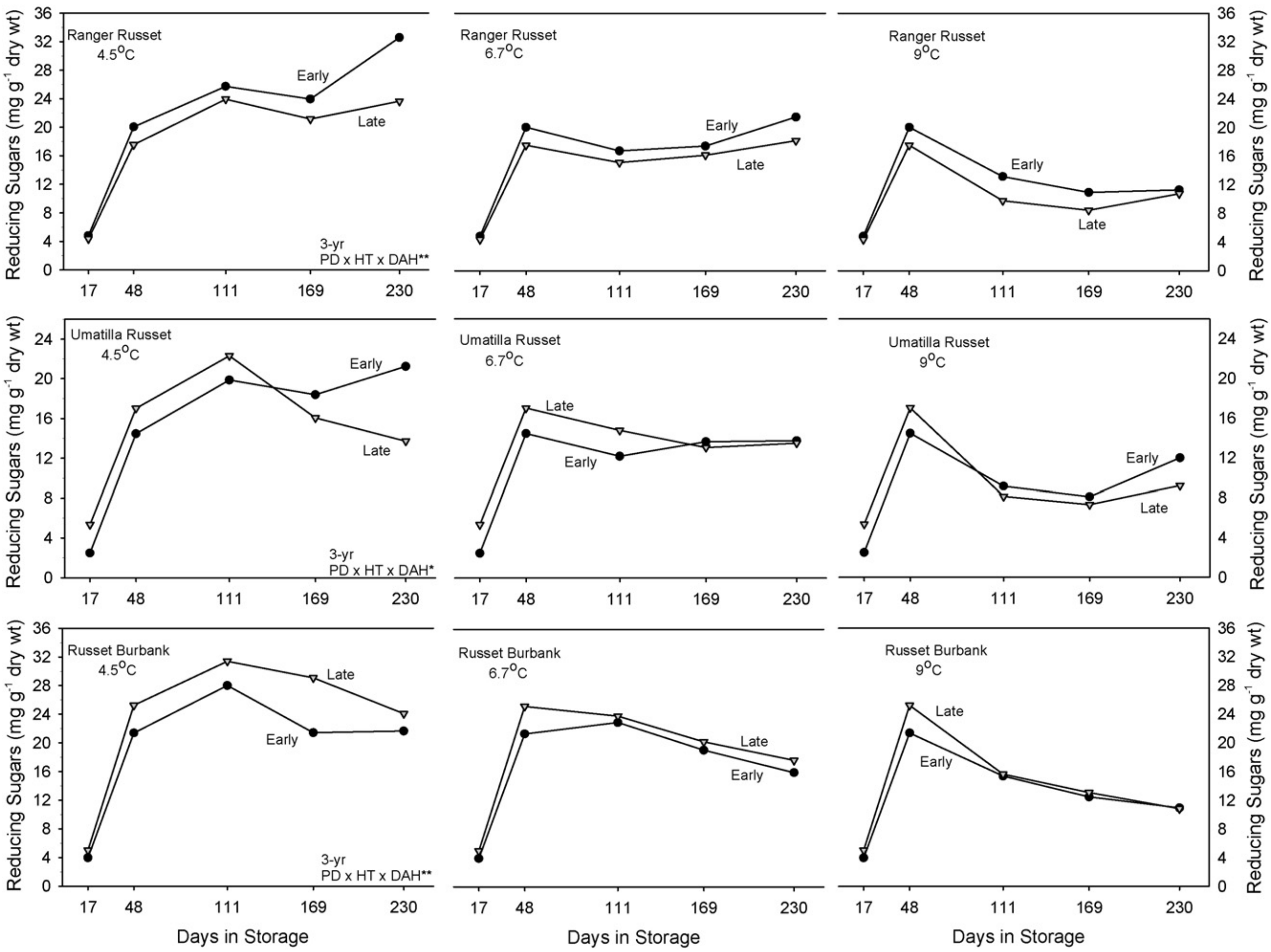

Fig. 5. Changes in reducing sugar concentrations of 'Ranger Russet' (top), 'Umatilla Russet' (middle), and 'Russet Burbank' (bottom) tubers as affected by planting date (PD), holding temperature (HT), and days after harvest (DAH). Data has been averaged over conditioning temperatures to show the significant PD × HT × DAH interactions for each cultivar (see Table 3). Each point is the average of 108 tubers over three storage seasons (2002–2004). $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$, respectively.

November) fell from 9 to 4.5 °C for tubers from both the early and late plantings (Fig. 6B–D and F–H). Furthermore, changes in the rates of sweetening with conditioning temperature depended on tuber maturity (planting date). Tubers from the late planting had higher concentrations of reducing sugars than those from the early planting after the 17 d wound-healing period (Table 2, Fig. 6) and the rates of sweetening increased 9.9- and 5.2-fold in tubers from the late and early plantings, respectively, as conditioning temperature fell from 9 to 4.5 °C (Table 4). Hence, the rates of reducing sugar accumulation increased by 118 and 166 $\mu g\,g^{-1}\,d^{-1}$ for every degree centigrade decrease in conditioning temperature in tubers from the early and late plantings, respectively. These differences reflect increased sensitivity of tubers from the late planting to sweetening when conditioned at 4.5 °C, relative to tubers from the early planting (Fig. 6B and F).

The concentrations of reducing sugars during the holding period (48–230 DAH) depended on temperature, with higher relative concentrations at lower temperatures regardless of conditioning temperature and planting date (Fig. 6; Table 3, HT × DAH, $P \leq 0.001$). Like 'Ranger Russet', reducing sugar concentrations in 'Umatilla Russet' tubers held at 4.5 °C were lower over the first 120 d of holding (from 48 to 169 d) when tubers had first been conditioned at 6.7 or 9 °C compared with continuous storage at 4.5 °C (CT × HT, $P \leq 0.01$) (Fig. 6C, D, G, and H). Moreover, the high reducing sugar concentrations in tubers conditioned at 4.5 °C fell significantly when storage temperatures were subsequently raised to 6.7 and 9 °C for the remainder of the 230 d storage period (Fig. 6B and F). These declines in reducing sugar concentrations were greatest in tubers from the late planting, likely due to the greater initial buildup in reducing sugars in these tubers in response to the 4.5 °C conditioning treatment (Fig. 6F). Interestingly, even those tubers that remained at 4.5 °C beyond the initial 48 d conditioning period acclimated to this low holding temperature, as evidenced by a decline in reducing sugar concentration over the subsequent 182 d of storage (Fig. 6A and E). This was especially apparent in tubers from the late planting where the reducing sugar concentration fell from 32 $mg\,g^{-1}$ (USDA 3 equivalent) at 48 DAH to 15 $mg\,g^{-1}$ (USDA 1 equivalent) by 230 DAH (Fig. 6E).

The effects of planting date on sweetening of 'Umatilla Russet' tubers were subtle and somewhat dependent on the holding temperature (Table 3, PD × HT × DAH, $P \leq 0.05$). Averaged over conditioning temperature, reducing sugar concentrations were higher in tubers from the late planting through the first 111 d of storage at 4.5 and 6.7 °C (Fig. 5). By 230 d of storage however, reducing sugar concentrations were higher in tubers from the early planting at 4.5 °C, and were equivalent in tubers from both plantings when stored at 6.7 °C. When stored at 9 °C, tubers from the late planting had higher reducing sugar concentrations than those from the early planting during the first 48 d of storage, but by 230 d, tubers from the early planting had higher concentrations than those from the late planting (Fig. 5). Reducing sugar concentrations decreased to 15 $mg\,g^{-1}$ dry wt or less in response to

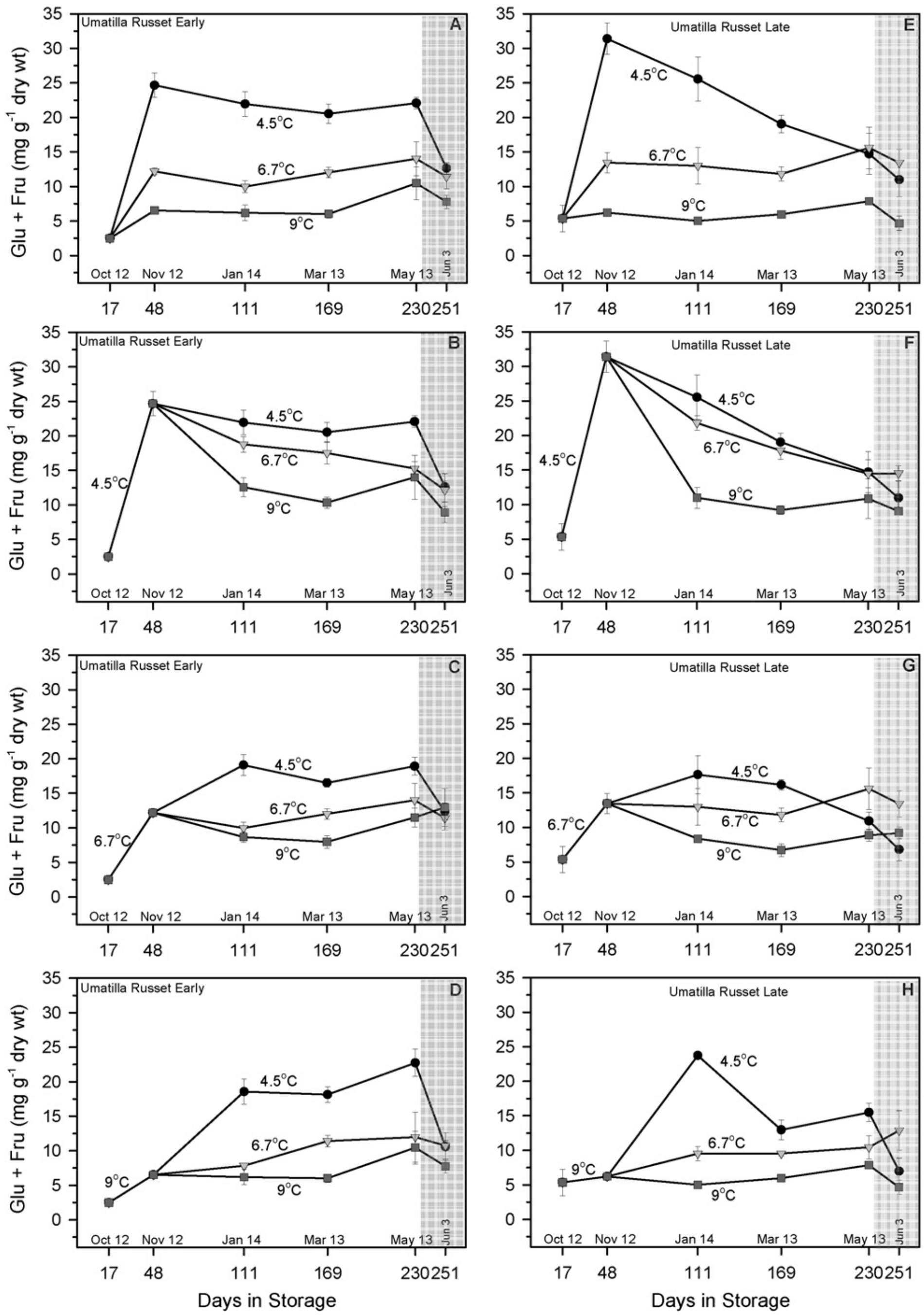

Fig. 6. Changes in reducing sugar (glucose + fructose) concentrations in 'Umatilla Russet' tubers of different maturity (planting date) in response to conditioning, holding, and reconditioning temperatures over 251 d of storage. Tubers from early (left column) and late plantings (right column) were harvested 25 September (163 and 133 d after planting), wound-healed at 12 °C (95% RH) for 17 d, and then placed at 4.5, 6.7 and 9 °C to condition for 31 d (12 October–12 November). Tuber samples from each conditioning temperature were subsequently stored at 4.5, 6.7 and 9 °C (holding) for an additional 182 d (until 13 May), resulting in nine conditioning/holding temperature combinations. Tubers were reconditioned (shaded) for 21 d at 16 °C (13 May–3 June) at the end of the study. Data are averaged over three storage seasons (n = 36, ±SE). ANOVA results are presented in Table 3.

reconditioning for 21 d at 16 °C at the end of storage (230–251 DAH) (Fig. 6).

3.3.3. cv. Russet Burbank

Like 'Ranger Russet' and 'Umatilla Russet', reducing sugar concentrations of 'Russet Burbank' tubers were affected by planting date, storage time, conditioning temperature, and holding temperature (Table 3). Sweetening of 'Russet Burbank' tubers increased as storage temperature decreased, with maximum sugar concentrations reached within the first month of storage in tubers from both plantings (Fig. 7A and E). Reducing sugars increased in tubers as the conditioning temperature (12 October–12 November) fell from 9 to 4.5 °C regardless of planting date (Fig. 7B–D and F–H). The average rates of sweetening were 1146, 551, and 125 $\mu g\,g^{-1}\,d^{-1}$ when conditioned at 4.5, 6.7, and 9 °C, respectively (Table 4). The rate of reducing sugar accumulation thus decreased by 227 $\mu g\,g^{-1}\,d^{-1}$ ($P \leq 0.01$) for every degree increase in conditioning temperature during this period.

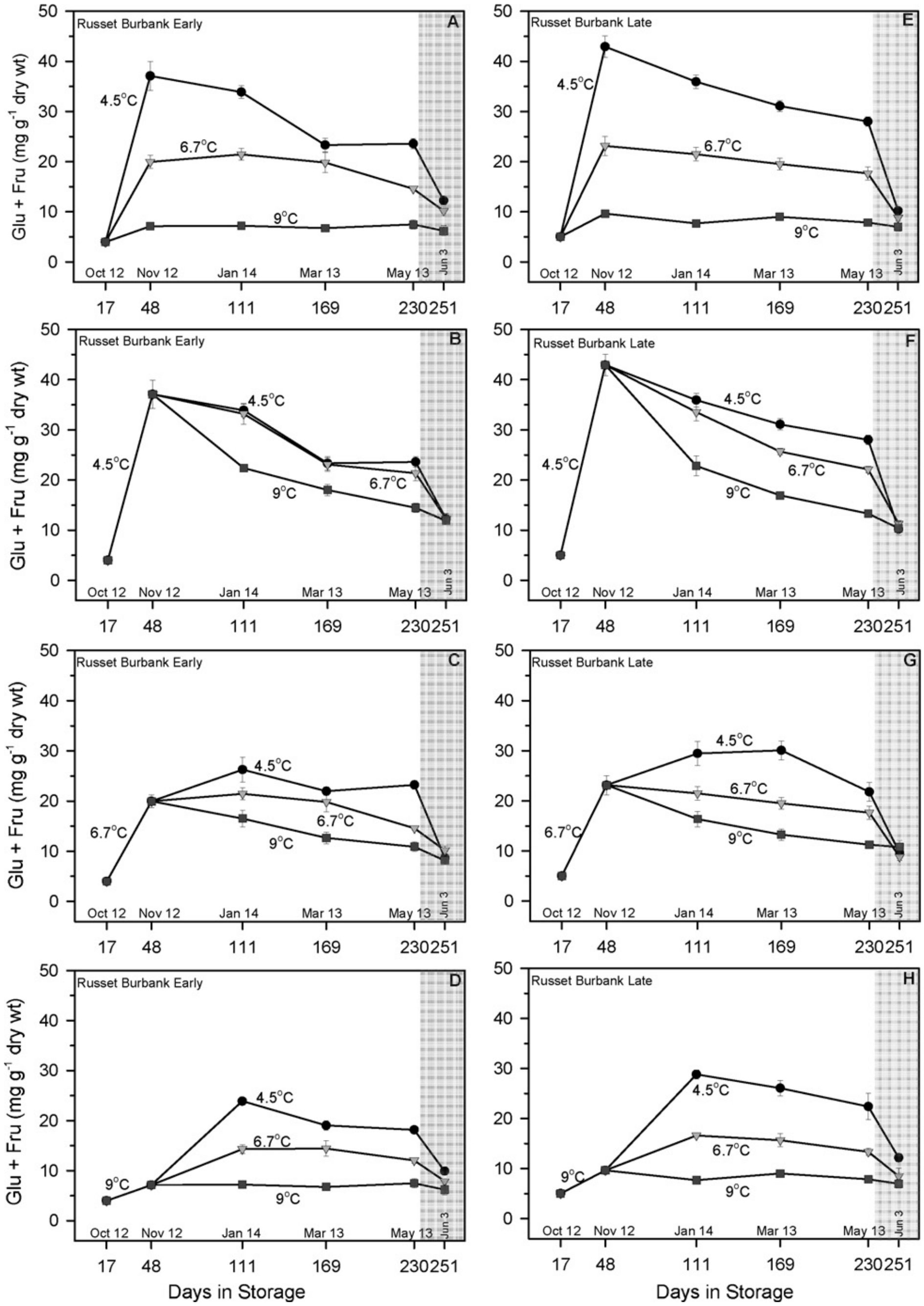

Fig. 7. Changes in reducing sugar (glucose + fructose) concentrations in 'Russet Burbank' tubers of different maturity (planting date) in response to conditioning, holding, and reconditioning temperatures over 251 d of storage. Tubers from early (left column) and late plantings (right column) were harvested 25 September (163 and 133 d after planting), wound-healed at 12 °C (95% RH) for 17 d, and then placed at 4.5, 6.7 and 9 °C to condition for 31 d (12 October–12 November). Tuber samples from each conditioning temperature were subsequently stored at 4.5, 6.7 and 9 °C (holding) for an additional 182 d (until 13 May), resulting in nine conditioning/holding temperature combinations. Tubers were reconditioned (shaded) for 21 d at 16 °C (13 May–3 June) at the end of the study. Data are averaged over three storage seasons ($n = 36$, ±SE). ANOVA results are presented in Table 3.

Consistent with the other cultivars, reducing sugar concentrations were higher at lower holding temperatures for most conditioning/holding combinations over the holding period (Fig. 7; Table 3, HT × DAH, $P \leq 0.001$). The only exceptions were tubers from the early planting conditioned at 4.5 °C and subsequently stored at 4.5 and 6.7 °C (Fig. 7B). These tubers had equivalent reducing sugar concentrations through the 182-d holding period. Like 'Ranger Russet', the reducing sugar concentrations in 'Russet Burbank' tubers stored at 4.5 °C were lower over the first 120 d of holding (from 48 to 169 d) if tubers were initially conditioned at 6.7 and 9 °C (CT × HT, $P \leq 0.001$) (Fig. 7C, D, G, and H). Additionally, reducing sugar concentrations in tubers conditioned at 4.5 °C (Fig. 7B and F) subsequently declined over the remainder of the storage period at all three holding temperatures regardless of planting date, and the rate of decline was higher for tubers held at 9 °C. versus those held at 6.7 and 4.5 °C.

Reducing sugar concentrations were higher in tubers from the later planting at 48 d after harvest regardless of conditioning temperature (Fig. 7F–H). On average, tubers from the late planting accumulated more reducing sugars than those from the early plant-

ing, particularly early in the storage season and in response to cold (4.5 °C) conditioning/holding temperatures (Figs. 5 and 7). The reducing sugar concentrations in tubers from all 6.7 and 4.5 °C holding temperature treatments fell significantly in response to reconditioning at 16 °C for 21 d (230–251 DAH), to values at or below 12 mg g^{-1} dry wt (USDA 0 equivalent) (Fig. 7).

4. Discussion and conclusions

Many factors interact to affect sugar accumulation in potato tubers during storage. Water stress during growth (Owings et al., 1978; Eldredge et al., 1996), heat stress (Timm et al., 1968), low fertility or nutrient stress (Iritani and Weller, 1978), tuber maturity at harvest (Miller et al., 1975; Pritchard and Adam, 1992), specific gravity (Iritani and Weller, 1976), storage temperatures (Burton, 1989; Hertog et al., 1997b), temperature management (Iritani and Weller, 1980) and cultivar, have all been shown to affect sweetening and thus processing quality during storage. Reducing sugars compromise tuber processing quality by reacting with free amino acids during frying, resulting in dark processed products with increased levels of acrylamide (Amrein et al., 2003). Reducing sugars are limiting for this reaction and therefore the color (lightness) and acrylamide levels in fried product are proportional to the concentrations of glucose plus fructose in tubers at the time of processing. Processors rate the color of processed fries from USDA 0 (lightest fries) to USDA 4 (darkest fries) (Anon., 1988). The approximate reducing sugar concentrations at which the color (Photovolt reflectance) of processed fries changes from USDA 0 to 1, USDA 1 to 2, USDA 2 to 3, and USDA 3 to 4 are 13-, 20-, 26-, and 35-mg g^{-1} dry wt, respectively. Note also that reducing sugars are inversely proportional to photovolt reflectance (RS = 69.9–2.766[Ref] + 0.03[Ref]^2; R^2 = 0.83, P < 0.001 [Driskill et al., 2007]). The frozen-processing industry rejects potatoes that process darker than USDA 2. Hence, reducing sugar (glucose + fructose) concentrations greater than 26 mg g^{-} dry wt (2.6%) are unacceptable. Reducing sugar concentration and thus color of processed product can also vary along the apical to basal axis of a tuber. The basal end typically has higher sugars than the apical end and stresses during growth can accentuate this difference, resulting in 'sugar ends' (Iritani and Weller, 1980). Therefore, uniformity of color is also a major consideration in evaluating the quality of processed product.

The purpose of this study was to investigate the effects of tuber maturity on the postharvest sweetening responses of the relatively new long-season russet cultivars, 'Ranger Russet' and 'Umatilla Russet', relative to the standard cultivar, 'Russet Burbank'. Tubers of different maturities were produced by varying the planting date and harvesting the crops simultaneously. As expected, the lengthier growing season (163 d) achieved by the early planting resulted in higher yields. The three cultivars, however, produced distinctive tuber size distribution profiles in response to planting date, likely due to cultivar-dependent differences in the duration of vine growth. 'Ranger Russet' maintains vine growth (150+ d) longer than 'Russet Burbank', which tends to senesce around 140 d. The lack of planting date-induced differences in yield of 'Russet Burbank' reflects the fact that both the early- and late-planted crops had reached maturity by vine kill (total vine senescence), while the late plantings of 'Ranger Russet' and 'Umatilla Russet' were still actively growing at vine kill (green vines). Yield and tuber size distributions were thus more affected by planting date in the latter two cultivars. 'Russet Burbank', 'Ranger Russet' and 'Umatilla Russet' achieve physiological maturity 150–155 d after planting in most years under the long-season growing conditions prevalent in the Columbia Basin (Knowles et al., 2008).

Several physiological characteristics of tubers were compared to document whether differences in tuber maturity were achieved by the staggered planting date approach. Tubers (227–284 g) from the late planting had higher sucrose concentrations than those from the early planting. Previous studies have shown that sucrose declines progressively during tuber growth and is typically higher in less mature tubers (Knowles et al., 2008). The maturation indices common to two out of three cultivars included tuber respiration rate immediately following harvest and time to dormancy break, both of which were increased in the late-planted crops. Reducing sugar content, French fry color, and specific gravity were of no general utility in establishing maturity differences following wound-healing, but may be useful in combination with the other three indices. Specifically, the number of physiological differences could be used collectively as an indicator of relative maturity in a comparison between two lots of the same cultivar. 'Ranger Russet' and 'Umatilla Russet' tubers from the late-planting exhibited four of six physiological characteristics different from tubers from the early planting. Hence, despite the fact that the 227–284-g tubers from the early and late plantings were morphologically indistinguishable, two crops of different maturity were achieved for these cultivars. 'Russet Burbank', however, was marked by only two of six characteristics, suggesting a smaller difference in maturity created by the two planting dates.

Tubers from the early and late plantings were subjected to a range of conventional and non-conventional storage temperature regimes over a 230-d storage period to assess the effects of tuber maturity on the sweetening responses for each cultivar. As expected, reducing sugars increased rapidly when tubers were conditioned at 4.5 °C immediately after wound-healing. Tubers of all three cultivars were most sensitive to cold-induced sweetening during the first 30–40 d after harvest. However, following the initial month at 4.5 °C, reducing sugar concentrations gradually declined in selected samples held continuously at this low temperature, reflecting partial acclimation. The extent of low temperature acclimation depended on cultivar and tuber maturity. 'Russet Burbank' and 'Umatilla Russet' acclimated the most to 4.5 °C, with constant declines in reducing sugar concentrations from 48 to 230 d. The relatively immature tubers from the late planting of 'Umatilla Russet' (grown for 133 d) acclimated to a greater extent than the chronologically older tubers from the early planting (grown for 163 d) (Fig. 6). 'Russet Burbank' tubers from the early and late plantings acclimated to constant storage at 4.5 °C with equivalent declines in reducing sugar concentrations from 48 to 230 d (Fig. 7). 'Ranger Russet' maintained high and relatively constant levels of reducing sugars at 4.5 °C through 230 d of storage regardless of planting date and thus maturity (Fig. 4).

Conditioning tubers at 6.7 and 9 °C (17–48 DAH) decreased their sensitivity to sweetening when subsequently stored at 4.5 °C (48–230 DAH) for all cultivars. On the other hand, tubers conditioned at 4.5 °C reconditioned during the holding period at 6.7 and 9 °C, resulting in acceptable sugar levels for processing later in the storage season (169–230 DAH). Knowledge of these responses potentially broadens the options for using non-conventional storage temperature regimes for managing potatoes in storage.

Tuber maturity affected the extent of sweetening during storage. 'Ranger Russet' tubers from the early planting accumulated higher concentrations of reducing sugars than those from the later planting under most temperature regimes. 'Ranger Russet' is thus sensitive to over-maturation in the field which, in contrast to the other cultivars, results in increased sweetening during storage; a characteristic of 'Ranger Russet' described anecdotally but never documented prior to these studies. Therefore, the time between vine kill and harvest should be minimized to maintain the lowest reducing sugar concentrations possible during storage of this

cultivar. While 'Ranger Russet' was hitherto regarded as a cultivar with a relatively short storage life (compared with 'Russet Burbank' and 'Umatilla Russet'), acceptable levels of reducing sugars (<25 mg g^{-1} dry wt) for frozen processing were maintained when stored for 230 d at 6.7 and 9 °C. Analyses of the processing qualities of all three cultivars in response to the nine temperature regimes support this result (Driskill et al., 2007).

In contrast to 'Ranger Russet', tubers from the late planting of 'Russet Burbank' and 'Umatilla Russet' were more sensitive to sweetening, particularly during conditioning at 4.5 °C, which likely reflects their relative immaturity compared with tubers from the early planting. The reducing sugar concentrations in tubers of all cultivars fell from 230 to 251 DAH in response to reconditioning at 16 °C and the extent of reconditioning was greater for 'Russet Burbank' and 'Ranger Russet' than for 'Umatilla Russet'. The decreased reconditioning response of 'Umatilla Russet' was likely affected by its greater inherent ability to acclimate to storage at 4.5 °C, resulting in lower reducing sugar concentrations at 230 d relative to the other cultivars. There is also evidence that 'Umatilla Russet' tubers age faster than the other cultivars, which would affect the ability to recondition late in storage due to the onset of irreversible senescent sweetening. Indeed, the ability of 'Umatilla Russet' tubers to recondition attenuates progressively over 230 d of storage (Driskill et al., 2007). Further research to determine the mechanism by which reconditioning ability is lost in this cultivar is warranted.

In summary, manipulating planting date resulted in tubers that had different rates of respiration, lengths of dormancy, and sucrose levels at harvest. While morphologically indistinguishable, tubers from the early and late plantings were thus physiologically different and were therefore of different maturities. Tuber maturity affected the sweetening responses to a wide range of storage temperature regimes. Non-conventional temperature regimes were identified that resulted in reducing sugar levels that, on average, would be acceptable for processing quality over a prolonged storage season. Tubers of all cultivars were most sensitive to low temperature sweetening (LTS) during the first 48 d of storage. Conditioning temperatures of 6.7 and 9 °C during the initial month after wound-healing reduced the sensitivity of tubers to subsequent sweetening during prolonged storage at 4.5 °C. 'Umatilla Russet' and 'Russet Burbank' tubers from the late planting (grown 133 d) were more sensitive to LTS (4.5 °C) initially during storage than those from the early planting, likely reflecting their relative immaturity. Conversely, 'Ranger Russet' tubers from the late planting were more resistant to LTS than those from the early planting, indicating increased sensitivity of the latter to over maturation and underscoring the importance of harvesting 'Ranger Russet' prior to total vine senescence (i.e. harvesting green). 'Russet Burbank' and 'Ranger Russet' recondition better than 'Umatilla Russet' following 230 d of storage.

The temperature grid protocol presents a thermal challenge to evaluate cultivar-dependent differences in sweetening phenotype and retention of processing quality during storage. Commercial potato storages are not capable of the instantaneous changes in temperature employed in the grid protocol. The gradual rise and decline in temperatures in these facilities would certainly delay the sweetening response of tubers compared to the results obtained herein. For example, the rapid sweetening observed in all cultivars during conditioning at 4.5 and 6.7 °C in this study would be characterized by a slower rate of increase to relatively high levels if the temperature decline from wound-healing to conditioning temperatures were to take place over a longer period. The temperature grid protocol is ideal for characterizing the full range of sweetening responses in newly released cultivars and tubers of different maturities.

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